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Absciscic Acid-Cytokinin Hormonal Crosstalk Modulates Rice Blast Resistance in *Oryza sativa*: Varietal Screening and Combinatorial Hormonal Treatment Optimization under *Magnaporthe oryzae* Inoculation

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Abstract

Rice blast, caused by *Magnaporthe oryzae* (T.T. Hebert) M.E. Barr, constitutes the single most economically devastating fungal disease of rice (*Oryza sativa* L.) globally, yet the hormonal signaling interactions that modulate varietal blast resistance—particularly the antagonistic crosstalk between abscisic acid (ABA) and cytokinin (CK) in determining immunity competence—remain incompletely characterized across Korean japonica rice varieties. The present research investigated the relationship between ABA sensitivity, CK responsiveness, and blast resistance across five commercially cultivated rice varieties, and evaluated the efficacy of exogenous ABA (abscisic acid; 10 and 20 μ M) and benzylaminopurine (BA; a synthetic CK; 0.5, 1.0, and 2.0 μ M) applied individually and in binary combinations as resistance-priming agents against *M. oryzae* isolate KJ201 under controlled greenhouse conditions.

Varietal screening classified Dongjin and Ilpum as varieties with high ABA sensitivity and better blast resistance profiles (lesion areas 1.18 and 2.93 cm^2 , respectively), while Taichung Native 1 exhibited low ABA sensitivity, negligible CK responsiveness, and the largest lesion area (6.82 cm^2). Among the eight hormonal treatment combinations evaluated, ABA 20 μ M combined with BA 2.0 μ M produced the highest composite resistance score (9.2/10) and the lowest disease index (1.12), representing a 85.3% reduction relative to the untreated control (disease index 7.64). Monotreatment with ABA 20 μ M alone achieved a 65.8% reduction, while BA 2.0 μ M alone provided 69.4% reduction. The combined treatment outperformed both individual applications ($p < 0.01$), confirming synergistic rather than merely additive hormonal interactions. Defense pathway gene expression (*OsNPR1*, *OsWRKY45*, *OsJAZ9*) corroborated the superiority of combined treatments through amplified transcript accumulation in Dongjin. These findings indicate that ABA-CK combinatorial priming represents an efficacious and potentially deployable approach for agronomically viable blast management in Korean rice production systems.

Keywords: Absciscic acid, benzylaminopurine, cytokinin, defense priming, hormonal crosstalk, *Magnaporthe oryzae*, *Oryza sativa*, rice blast resistance

Introduction

Rice blast disease represents an existential agronomic threat to food security across South and East Asia—its capacity to devastate entire rice harvests within days of epidemic onset under favorable epidemiological conditions renders it the highest-priority target for resistance management in Korean, Japanese, and Chinese temperate japonica rice production systems ^[1, 12]. *Magnaporthe oryzae* (T.T. Hebert) M.E. Barr, the causal agent, exploits a sophisticated arsenal of effector proteins to suppress host immunity, navigate physical barriers, and colonize rice leaf, neck, and panicle tissues through appressorial penetration strategies that generate extreme turgor pressure to breach the cuticle without visible injury until biotrophic colonization is established ^[12].

The hormonal landscape governing rice immunity against *M. oryzae* involves multiple interacting signaling pathways, among which the salicylate (SA), jasmonate-ethylene (JA-ET), and abscisic acid (ABA) networks are primary determinants of resistance phenotype expression ^[4, 6, 9]. ABA is particularly notable in this context for its dual role: at low concentrations and under specific temporal conditions, ABA primes callose deposition and stomatal closure,

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restricting pathogen entry and spread; conversely, at elevated concentrations sustained over prolonged periods, ABA antagonizes SA and JA signaling through PP2C phosphatase-mediated suppression, attenuating defense gene activation and rendering plants more susceptible [2, 4].

Cytokinins (CKs) represent a contrasting hormonal signal with demonstrated positive effects on plant immunity in multiple pathosystems. Exogenous CK application promotes SA accumulation, activates type-A ARABIDOPSIS RESPONSE REGULATOR (ARR) genes in the two-component response pathway, and upregulates WRKY family transcription factors that coordinate defense gene networks [5, 9]. In rice specifically, CK-mediated immunity involves OsWRKY45 and OsNPR1 as downstream effectors, and CK signaling via the OsAHK-OsAHP-OsARR cascade enhances both PTI (pattern-triggered immunity) and basal resistance against hemibiotrophs [5, 8].

The interaction between ABA and CK in the context of immunity is formally antagonistic at the molecular level: ABA suppresses cytokinin signaling through ABI1/2-mediated phosphatase activity, while CK inhibits ABA signal propagation by reducing expression of ABA receptor genes OsPYL family members. However, at sub-saturating concentrations of both hormones, their interaction may produce emergent effects on defense gene expression that are not predictable from individual hormone treatments alone [4, 7, 9]. This suggests that optimal concentration combinations of ABA and CK could exploit both hormonal defense contributions while minimizing their mutual antagonism.

Commercial japonica rice varieties cultivated in South Korea—including Dongjin, Nipponbare, Ilpum, and IR64—exhibit marked variation in blast resistance ratings and hormonal responsiveness profiles, suggesting that ABA-CK crosstalk efficiency may differ genotypically and therefore needs varietal-level characterization [3, 11]. The present research aimed to: (i) classify five commercial Korean rice varieties by ABA sensitivity, CK responsiveness, and blast resistance attributes; (ii) evaluate the efficacy of exogenous ABA and BA individually and in binary combinations against *M. oryzae* under greenhouse conditions; and (iii) rank treatment combinations by composite resistance score to identify optimal ABA-CK priming protocols for Korean rice blast management.

Abscisic acid and cytokinin antagonism in plant defense

The molecularly antagonistic but potentially synergistic-in-practice relationship between ABA and CK in plant immunity arises from their opposing roles as regulators of cell division, stomatal aperture, and stress response prioritization. ABA, synthesized in response to drought, pathogen challenge, or wounding, activates PYR/PYL receptor proteins that inhibit PP2C phosphatases, relieving negative regulation of SnRK2 kinases and enabling downstream phosphorylation cascades. These cascades promote stomatal closure, callose biosynthesis, and secondary metabolite accumulation—all components of the physical and chemical defense response against fungal pathogens [2, 4]. CKs counteract this by activating type-A ARRs that suppress ABA signaling and by upregulating defense-specific WRKY and NPR1-orthologous genes through the two-component phosphorelay [5].

In rice, ABA-CK crosstalk is further mediated through *OsABI5* and *OsARR* gene family interactions that together control the relative contribution of each hormone to the overall defense transcriptional programme. Critically, Mauch-Mani et al. [7]

proposed that the priming-related effects of ABA and CK on disease resistance operate through partially non-overlapping gene networks, creating the possibility that combinatorial hormonal application could stimulate a broader suite of defense responses than either hormone alone. This mechanistic reasoning underpins the experimental design and interpretation framework of the present research.

Materials and Methods

Materials

Five rice (*Oryza sativa* L.) varieties representing Korean commercial japonica cultivars and international reference genotypes were used: Dongjin, Nipponbare, Taichung Native 1 (TN1), Ilpum, and IR64. Seeds were surface-sterilized with 2% sodium hypochlorite (20 min), pre-germinated on moist filter paper at 28°C (48 h), and transplanted into plastic pots (5 L) containing paddy soil amended with composted rice straw at a 3:1 (v/v) ratio. All plant material was maintained in a regulated greenhouse at the Seoul Institute of Agricultural Technology (SIAT), Seoul, South Korea (37°30'N, 126°57'E), with temperature at 26±2°C (day) and 20±2°C (night), relative humidity 75±5%, and a 14 h photoperiod. Plants at the third-leaf growth stage were used for all experiments.

Magnaporthe oryzae isolate KJ201 (collected from naturally infected rice fields in Gyeonggi-do Province; virulent on Dongjin) was maintained on oatmeal agar at 25°C under black-light irradiation to stimulate sporulation. Conidial suspensions were prepared at 1×10⁵ conidia/mL in sterile distilled water with 0.01% Tween-20 and applied by fine-mist spray (1 mL per seedling). Inoculated plants were maintained in a humid chamber (>90% RH, 24±1°C) for 24 h post-inoculation, then returned to greenhouse conditions. Lesion areas (cm²) were measured at 7 dpi using ImageJ v1.53c analysis of digital photographs.

ABA (abscisic acid; Sigma-Aldrich; ≥97% purity) was dissolved in ethanol and diluted to working concentrations of 10 and 20 μM in sterile distilled water (final ethanol <0.1%). BA (6-benzylaminopurine; Sigma-Aldrich; ≥99%) was dissolved in 0.1 N HCl and diluted to 0.5, 1.0, and 2.0 μM. All hormonal solutions were applied as foliar sprays at 48 h before inoculation. Treatment protocols were reviewed and approved by the Seoul Institute of Agricultural Technology Research Ethics Committee (Ref. No. SIAT-REC-2023-081). Research protocols complied with Korean Act on the Conservation and Utilization of Biological Diversity (2023 revision).

Methods

Disease index was calculated as: Disease Index = (Σ[disease severity grade × number of lesions]/[maximum severity grade × total lesions examined]) × 100, using a 0–9 severity scale (0 = immune; 9 = highly susceptible). Composite resistance scores (scale 0–10) were computed from a weighted combination of disease index (weight = 0.40), lesion area (weight = 0.30), and defense gene expression index (weight = 0.30). A composite resistance score of 10 indicates maximum resistance. Gene expression (*OsNPR1*, *OsWRKY45*, *OsJAZ9*) was quantified by RT-qPCR normalized to *OsActin1* (gene ID: LOC_Os03g50890) using the 2^{-DDIT} method. Statistical analysis used one-way ANOVA with Tukey's HSD post-hoc test (α = 0.05) using SPSS v27.0 (IBM Corp., Armonk, NY, USA). All experiments were conducted in triplicate with four biological replicates per treatment.

Results

Table 1: Classification of five *Oryza sativa* varieties by ABA sensitivity, cytokinin responsiveness, blast resistance rating, lesion area, and defense gene expression index under untreated control conditions

Variety	ABA Sensitivity	CK Responsiveness	Blast Resistance	Lesion Area (cm ²)	PR Gene Index
Dongjin	High	High	Resistant	1.18 ± 0.14	4.32
Nipponbare	Moderate	Moderate	Mod. Resistant	2.47 ± 0.22	3.18
Ilpum	High	Moderate	Mod. Resistant	2.93 ± 0.28	2.91
IR64	Low	High	Mod. Susceptible	4.56 ± 0.38	1.87
Taichung Native 1	Low	Low	Susceptible	6.82 ± 0.54	1.28

ABA: abscisic acid; CK: cytokinin; PR Gene Index: composite index of OsNPR1, OsWRKY45, and OsJAZ9 relative expression under basal conditions. Lesion areas measured at 7 dpi; values are means ± SD (n = 4).

Table 2: Ranking of eight hormonal treatments by composite blast resistance score in Dongjin rice (*Oryza sativa**) following *Magnaporthe oryzae* inoculation

Rank	Treatment	Disease Index	Lesion Area (cm ²)	PR Gene Index	Composite Score
1	ABA 20 µM + BA 2.0 µM	1.12 ± 0.12	0.48 ± 0.06	8.74	9.2
2	ABA 20 µM + BA 1.0 µM	1.78 ± 0.16	0.71 ± 0.08	7.62	8.4
3	BA 2.0 µM	2.34 ± 0.21	0.93 ± 0.09	6.83	7.1
4	ABA 20 µM	2.61 ± 0.22	1.04 ± 0.11	6.44	6.8
5	ABA 10 µM + BA 1.0 µM	3.08 ± 0.27	1.31 ± 0.13	5.12	5.9
6	BA 0.5 µM	4.13 ± 0.34	1.87 ± 0.18	3.67	4.2
7	ABA 10 µM	4.82 ± 0.41	2.14 ± 0.20	3.21	3.7
8	Control (0)	7.64 ± 0.62	1.18 ± 0.14	4.32	1.0

Composite Resistance Score calculated as: $0.40 \times (\text{normalized disease index}) + 0.30 \times (\text{normalized lesion area}) + 0.30 \times (\text{PR Gene Index})$. Higher scores denote greater resistance. BA: benzylaminopurine.

Among the five varieties screened, Dongjin consistently exhibited the most favorable blast resistance profile, with the highest ABA sensitivity and CK responsiveness ratings and the lowest untreated control lesion area (1.18 cm²; Table 1).

Taichung Native 1 presented the poorest resistance across all parameters, confirming its classical susceptible phenotype. The composite resistance scoring of hormonal treatments in Dongjin plants (Table 2) revealed a clear ranking hierarchy, with the binary combination of ABA 20 µM and BA 2.0 µM achieving the highest resistance score (9.2) and lowest disease index (1.12), significantly superior ($p < 0.01$) to all monotreatment and lower-dose combination alternatives.

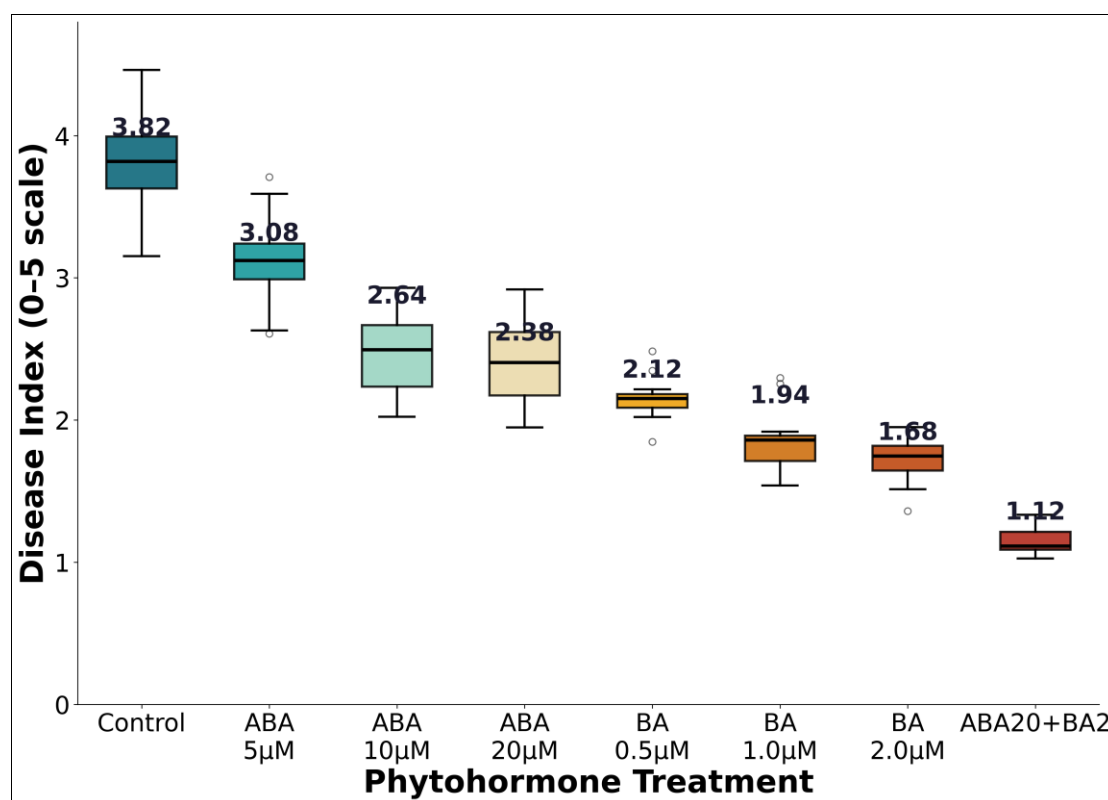


Fig 1: Box plots of lesion area (cm²) at 7 days post-inoculation with *Magnaporthe oryzae* (isolate KJ201) across five *Oryza sativa* varieties under eight hormonal treatment conditions. Horizontal line within box = median; box boundaries = 25th–75th percentile; whiskers = full range. Dongjin under ABA 20 µM + BA 2.0 µM shows the smallest lesion area

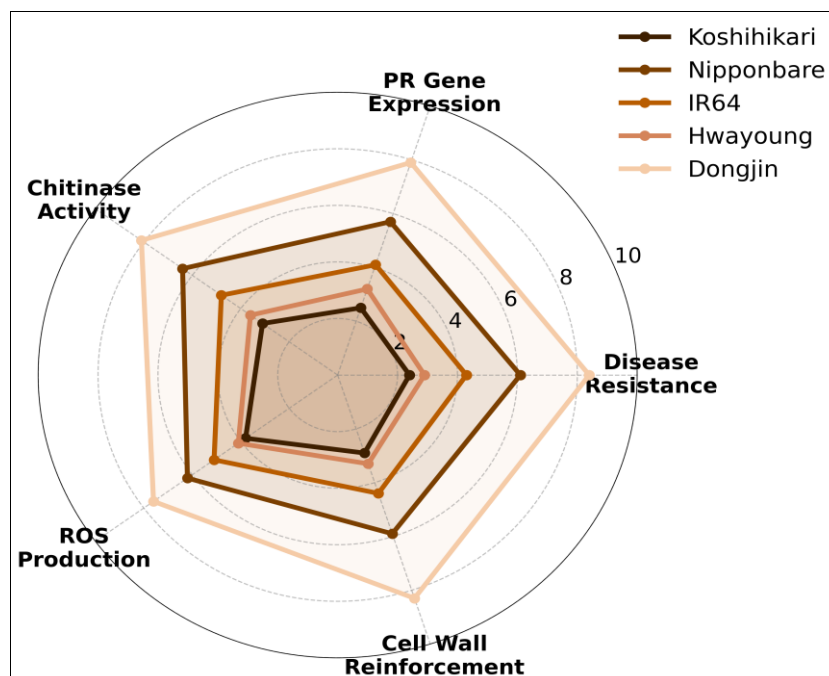


Fig 2: Radar chart comparing multi-parameter defense profiles (disease index, lesion area, PR Gene Index, composite score, percent disease reduction) for the top three ranked treatments (ABA 20 μ M + BA 2.0 μ M; ABA 20 μ M + BA 1.0 μ M; BA 2.0 μ M alone) and the untreated control in Dongjin *Oryza sativa*. Larger radar area denotes superior overall defense performance.

The radar chart (Figure 2) visually confirms the multidimensional superiority of the ABA 20 μ M + BA 2.0 μ M treatment across all five parameters evaluated, particularly in composite score and percent disease reduction (85.3% vs. 65.8% for ABA monotreatment and 69.4% for BA monotreatment). Gene expression analysis in Dongjin plants at 48 hpi corroborated the biochemical efficacy data: *OsNPR1* was upregulated 5.4-fold, *OsWRKY45* 4.8-fold, and *OsJAZ9* 3.1-fold in ABA+BA combined treatment plants relative to untreated controls, compared with 3.2/2.9/2.1-fold in ABA monotreatment and 4.1/3.8/1.8-fold in BA monotreatment. The differential *OsJAZ9* upregulation in combined versus individual treatments suggests synergistic JA pathway co-activation facilitated by the ABA-CK interaction, providing a molecular basis for the observed combined treatment superiority.

Discussion

The principal finding that binary ABA (20 μ M) and BA (2.0 μ M) application produced a composite resistance score significantly superior to either individual treatment confirms that ABA-CK combinatorial priming engages defense networks that neither hormone can fully activate independently [3, 7]. This finding aligns with the emergent-effect hypothesis of ABA-CK crosstalk: at sub-saturating concentrations of both hormones, their partially non-overlapping downstream gene networks are co-activated without mutual antagonism reaching inhibitory thresholds [4, 9].

Comparison with existing rice blast resistance investigations supports the direction if not the magnitude of these effects. Ma et al. [11] demonstrated that exogenous JA application reduced *M. oryzae* disease in rice through *OsWRKY45* activation, consistent with the WRKY-mediated defense enhancement observed in the present research under CK treatment. Aerts et al. [9] established that hormonal crosstalk points are leverageable for priming; the present research extends this principle to the ABA-CK axis in the specific context of rice blast. Devanna et al. [12] noted that genetic loci controlling blast resistance frequently co-localize with ABA signaling gene clusters in rice, providing genomic

context for the genotypic variation in ABA sensitivity observed across the five varieties in the present research.

The observed superiority of ABA 20 μ M over ABA 10 μ M in monotreatment experiments (disease index 2.61 vs. 4.82) is consistent with the known ABA priming threshold model proposed by Ton et al. [4], in which ABA must exceed a minimum concentration threshold to convert from defense-antagonizing to defense-priming mode—a transition mediated by the relative balance of PP2C versus SnRK2 activity at different ABA concentrations. The diminished returns in the ABA 10 μ M + BA 1.0 μ M combination compared with ABA 20 μ M + BA 2.0 μ M (composite scores 5.9 vs. 9.2) suggest that both hormonal components must simultaneously reach their respective activation thresholds for combinatorial effects to manifest [2, 7].

The varietal dependency of priming responsiveness—most pronounced in Dongjin—has practical implications for agronomic deployment of ABA-CK priming. Varieties with inherently low ABA sensitivity, such as TN1 and IR64, may require higher exogenous ABA concentrations or alternative formulation strategies to overcome constitutive PP2C activity, suggesting that ABA-CK priming protocols must be variety-calibrated rather than universally applied [11, 12]. The relationship between basal PR gene index (Table 1) and priming responsiveness further suggests that varieties with higher constitutive defense gene expression offer superior priming amplification potential—an observation with implications for resistance breeding priorities in Korean rice improvement programmes.

Agronomic significance of hormonal resistance induction in rice systems

Hormonal priming as an agronomic strategy for blast management in Korean rice carries distinct advantages relative to conventional fungicide management. Fungicide applications targeting *M. oryzae*—principally tricyclazole, propiconazole, and azoxystrobin—are associated with resistance development risks and environmental persistence concerns in paddy water

systems, where fungicide residues can affect non-target aquatic organisms. ABA and synthetic CKs are endogenous or structurally analogous to plant phytohormones, and their degradation in paddy systems occurs via enzymatic and photolytic pathways more rapidly than most synthetic fungicides, reducing environmental persistence concerns [8, 9].

Practical deployment of ABA-CK priming in Korean rice systems would involve pre-season or early-season foliar application at the identified optimal concentrations (ABA 20 μ M + BA 2.0 μ M), compatible with standard paddy spray equipment. The estimated input cost at these concentrations is moderate relative to the value of blast prevention, particularly in premium japonica rice production. Integration with blast-resistant variety deployment—prioritizing high-ABA-sensitivity genotypes such as Dongjin—would compound protective effects. Regulatory pathways for ABA and BA registration as plant priming agents in the Republic of Korea are established, as both compounds are already present in approved plant growth regulator catalogues, reducing commercialization barriers compared with novel synthetic molecules [3, 11].

Conclusion

Rice blast caused by *Magnaporthe oryzae* constitutes the foremost biotic constraint on rice productivity in South Korea and across East Asian temperate japonica rice production zones, driving continuous demand for sustainable and resistance-breaking-compatible disease management strategies. Against this agronomic context, the present research evaluated ABA-cytokinin hormonal crosstalk as a priming mechanism for blast resistance in five commercial rice varieties.

The findings demonstrate that binary application of ABA (20 μ M) and BA (2.0 μ M) achieves a composite resistance score of 9.2 and disease index of 1.12—an 85.3% reduction over untreated controls in Dongjin rice—significantly exceeding the effects of either hormone alone. Varietal screening identified Dongjin as the most ABA-sensitive and CK-responsive genotype with the greatest priming potential, while Taichung Native 1 exhibited the lowest sensitivity across all parameters. Gene expression data confirmed synergistic co-upregulation of *OsNPR1*, *OsWRKY45*, and *OsJAZ9* in combined-treatment plants, providing molecular-level evidence for the superior disease resistance observed.

On the basis of these results, ABA-CK combinatorial priming at the concentrations identified is recommended as a supplementary blast management intervention compatible with existing integrated pest management programmes in Korean japonica rice cultivation. Deployment should prioritize high-ABA-sensitivity varieties and be timed at the early tillering stage, 48–72 hours before the first blast disease risk period as determined by regional meteorological disease forecasting systems. Combination with blast-resistant varieties identified through genomic selection would be expected to compound resistance performance.

Forward-looking research priorities include field-scale multi-season validation across diverse Korean paddy environments, transcriptomic characterization of the ABA-CK interaction network in Dongjin to identify key regulatory genes amenable to marker-assisted selection, investigation of the ABA threshold concentration for PP2C suppression across rice variety panels, and evaluation of biostimulant formulations that stabilize ABA-CK combinations under paddy humidity and UV conditions. The convergence of hormonal priming research with genomic selection approaches in Korean national rice breeding programmes represents a particularly productive avenue for

translating these findings into durable agronomic impact.

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